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REDISCOVERY OF THE ENIGMATIC COELENTERATE *DENDROBRACHIA*, (OCTOCORALLIA: GORGONACEA) WITH DESCRIPTIONS OF TWO NEW SPECIES

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Since 1876, *Dendrobrachia fallax* Brook, an arborescent, noncalcareous anthozoan coelenterate with a spiny, proteinaceous axis, has been assigned to the suborder Antipatharia in spite of such equivocal features as the probable presence of eight pinnately branched tentacles and a solid axial core. In recent years, specimens resembling *D. fallax* have been collected from off the southern coast of Australia and from the Straits of Florida. These specimens represent two new species of *Dendrobrachia* and are here described as *D. paucispina* sp. nov and *D. multispina* sp. nov. Furthermore, anatomical and histological studies demonstrate that *Dendrobrachia* has characteristic octocorallian features. The solid, noncalcareous axis and absence of calcareous sclerites suggest a relationship with the holaxonian family Chrysogorgiidae, but the distinctive skeletal features warrant retaining the genus in a separate family Dendrobrachiidae.

KEY WORDS: Gorgonacea, Octocorallia, Antipatharia, Chrysogorgiidae, Dendrobrachiidae, *Dendrobrachia*.

Introduction

On 27 March 1876, at 8°03'S, 14°27'W, off Ascension Island, H.M.S. "Challenger" dredged two specimens of an arborescent coelenterate with spiny proteinaceous axis at station 343 in 425 fathoms of water. These specimens subsequently were described as *Dendrobrachia fallax* by Brook (1889) and assigned to a new family, Dendrobrachiidae, placed in the suborder Antipatharia. The species was taken again in 1901, off the Cape Verdes by the Prince of Monaco, and reported briefly by Thomson (1910), who concurred with Brook in placing it in a special family of Antipatharia.

In spite of their equivocal features — pinnate tentacles probably eight in number, absence of a hollow axial core — the spiny axis and lack of calcareous spicules overrode other considerations and classification of *Dendrobrachia* among the Antipatharia has prevailed until the present.

During 1988 and 1989, Karen Gowlett-Holmes, while aboard trawlers in the Great Australian Bight and farther south off the Continental shelf of Australia, collected a number of deep sea octocorals and antipatharians which were deposited in the South Australian Museum. Along with specimens of *Chrysogorgia* were six colonies also tentatively identified as chrysogorgiid gorgonians. When examined more closely, these were found to resemble Brook's enigmatic *Dendrobrachia fallax*. This new material represents a new species of the genus, and is sufficiently well preserved to permit a more detailed description of the soft anatomy and a reevaluation of the placement of the family Dendrobrachiidae. Also included in this report is a description of a new species of *Dendrobrachia* from the western Atlantic, which is based on one specimen collected from the Straits of Florida.

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Systematics

Subclass Octocorallia
Order Gorgonacea
Suborder Holaxonia
Family Dendrobrachiidae Brook, 1889
Genus *Dendrobrachia* Brook, 1889

Dendrobrachia Brook, 1889:159; Hickson, 1895:40; Thomson, 1910:142.

Type species: Dendrobrachia fallax Brook, by monotypy.

Diagnosis: Arborescent Gorgonacea with purely proteinaceous axis lacking hollow core; axis marked by conspicuous ridges and grooves, with more or less numerous and prominent spines along the summit of the ridges. Polyps and coenosarc without calcareous sclerites.

Distribution: Eastern Atlantic Ocean off Ascension and Cape Verde Islands; western Atlantic off Cay Sal, Bahamas; Great Australian Bight. 394-1089 m.

Dendrobrachia fallax Brook
FIGS 1, 2; Table 1

Dendrobrachia fallax Brook, 1889:159-160, pl. 10, figs 1-8. Thomson, 1910:142-143.

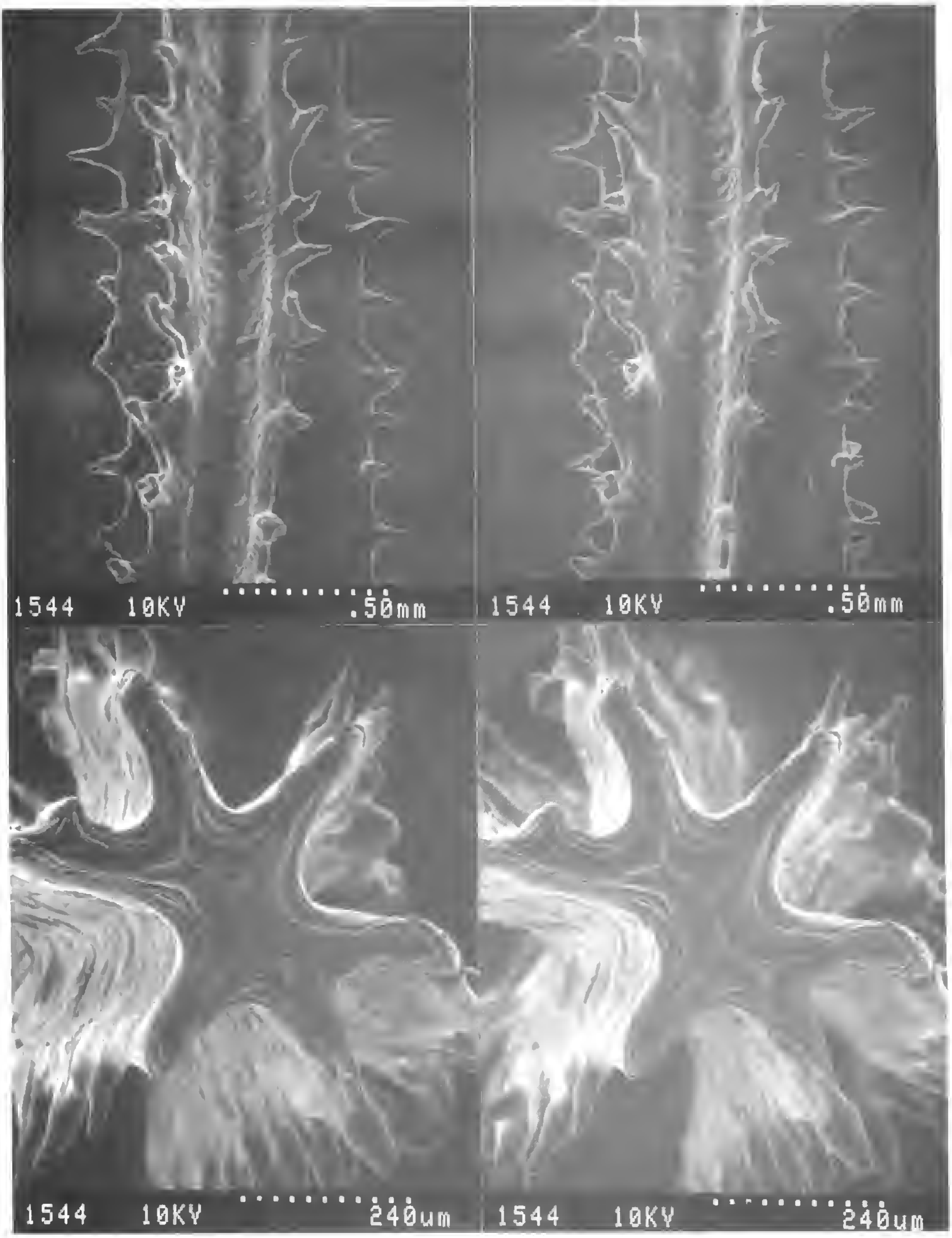


Fig. 1. *Dendrobrachia fallax* Brook, axis. Top, lateral view of terminal twig; bottom, cross section below apex. Stereoscopic pairs, SEM.

Material Examined: Type specimens, South Atlantic, off Ascension Island, 8°03'S, 14°27'W, 425 fm (777 m), "Challenger" Expedition, Sta. 343, 27 March 1876, 2 spec. (British Museum (BMNH) 1890.4.9.27).

Description: Colony planar, sparsely branched, with some overlapping of adjacent branches; branchlets bilateral, very irregularly alternate, rarely opposite, highest order branchlets mostly 1-3 cm long, occasionally longer, 0.5-0.8 mm in diameter, on average about 1 cm apart on same side of branches. Usually six, occasionally five or seven axial ridges on branchlets, increasing in number on larger branches. Spines present on ridges, one row per ridge; spines variable in size and shape but increasing in size with increasing thickness of branches, 0.2-0.25 mm long on branches about 1 mm in diameter. Polyps placed bilaterally, alternate or in nearly opposite pairs, 3-6 polyps per cm.

Discussion: Neither of the type specimens has a basal holdfast and one specimen appears to have been broken off a larger colony. Both specimens are about 20 cm tall and 5-10 cm wide. The basal "stem" diameter is 2 × 2.5 mm in one colony and about 3 mm in the other. Overall, the branching of the colonies is sparse, open, to about the eighth order, and generally in one plane with some overlapping of adjacent branches (see Brook 1899: p. 10, fig. 1). On the central portions of the corallum, the branching is very weakly sympodial in that some of the higher order ramifications become thicker and longer than the branches from which they arise. The branch angles (delineated by the inner or distal side of a branch and the lower order branch from which it arises) are generally greater than 45°. The smallest ramifications of the corallum, the branchlets, occur at all levels of the corallum. They are straight or slightly curved upward, unbranched, about 0.5-0.8 mm in diameter, and usually not more than 3 cm long. They tend to be positioned bilaterally and in a very irregularly alternating pattern along the sides of the branches. The distance between the bases of adjacent branchlets and/or branches on the same side of the lower order ramification from which they arise ranges from about 6-19 mm, and the average distance is 9.4 mm (n = 24). The distance between adjacent branchlets and branches on opposite sides of the axis ranges from about 2-17 mm, and the average distance is 6.3 mm (n = 25).

At the tips of the smallest branchlets the skeletal axis has six (occasionally five or seven) longitudinal ridges separated by grooves or channels. The ridges do not radiate out from a common central point, but rather appear to develop as bifurcations at the ends of a primary skeletal plate which is narrow and rectangular in cross section. This primary axial structure of branchlets can be seen at the core of the thicker branchlets when viewed in cross section (Fig. 1, bottom).

Extending down from the tips of the branchlets for a distance of about 1-1.5 cm, the ridges remain smooth or possess only small, scattered rounded elevations about 0.05-0.08 mm high. Further down on the branchlets distinct spines develop along the ridges (Fig. 1, top). Although the spines are not strictly uniform in size or shape throughout the corallum, they generally become longer as the diameter of the branchlets and branches increases. Many spines typically have a relatively sharp apex and a flared base (Fig. 2); however, others are more blunt, and some even have a swollen or knob-like apex. On branchlets 0.6-0.8 mm in diameter, the spines are usually 0.10-0.15 mm high; on branches 0.8-1.0 mm in diameter, they are usually 0.15 to 0.20 mm high (but up to 0.25 mm in some places). They are arranged in 5 to 6 rows (one row per skeletal ridge) with 4-5 spines per millimeter in each row. Generally, the ridges remain relatively narrow with a single row of spines. On the thicker branches more longitudinal rows of spines develop. On a branch 1.2 mm in diameter (excluding spines), the spines are about 0.3 mm high, 5-6 rows of spines can be seen in one lateral view, and there are about 3-4 spines per millimeter in each row. The height of the spines near the base of the stem (diameter 2.0 mm) is about 0.5 mm; there are 3-4 spines per millimeter in each row, and about 12 very irregular rows of spines can be seen in one lateral view. The rows are separated by wavy lines of coenenchyme which intersect one another at varying intervals. On the second specimen (basal stem diameter about 3mm), the spines reach a maximum size of about 0.4 mm, and as many as 17 rows of spines can be seen from one aspect. In the illustration given by Brook (1889: pl. 10, fig. 8) there appear to be about 38 or more rows around the entire circumference of a branch from near the base of the corallum.

The polyps arise from the coenenchyme in the grooves formed between the skeletal ridges. Their arrangement on the corallum is not strictly regular, although it is generally bilateral. On some branchlets a regular alternating pattern can be seen with the polyps spaced about 5 mm apart. Occasionally the polyps occur in nearly opposite pairs. In the latter case there can be as many as 6 polyps per centimeter along the branchlets. The condition of the polyps in both specimens is poor and allows for only a rough estimate of their size. They appear to be no taller than about 2-2.5 mm (including tentacles). The body column is about 1.0 mm in length and about 0.5 mm in diameter at the base. As noted by Brook, the polyps do not appear

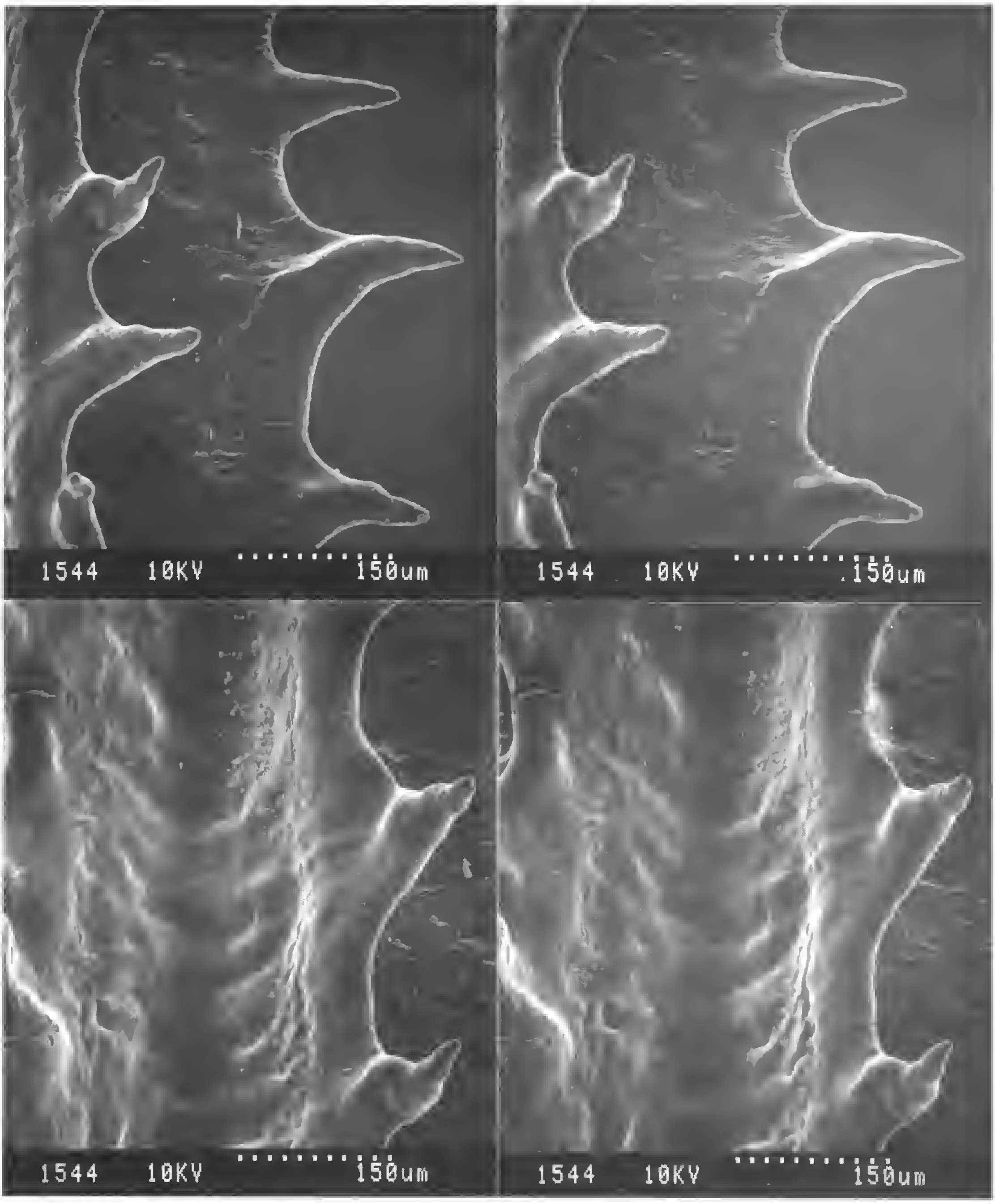


Fig. 2. *Dendrobrachia fallax* Brook, axis. Stereoscopic views of axial spines, SEM.

TABLE 1. *Morphometrics for* Dendrobrachia *spp.*

Parameter	*fallax*	*paucispina*	*multispina*
Corallum:			
Stem diam./height (%)	1.2-1.5	1.1-1.7	0.7[a]
Branchlets:			
Maximum length[b] (cm)	ca. 3	ca. 3	ca. 3
Diameter (mm)	0.5-0.8	0.4-0.8	0.4-0.5
Avg dist. apart[c] (mm)	9.4	9.0-9.5	13
Axial Ridges:			
Number on branchlets[d]	5,*6*,7	*6*,7,8	5
Axial Spines:			
Number of rows per ridge	1	0-1	1-2+
Number per mm per row[d]	3,*4*,5	3,*4*,5	*4*,5,6
Height of Spines[e] (mm):			
Axis diam. ≤0.5 mm	0.05-0.10	-	0.06-0.12
Axis diam. 0.6-0.8 mm	0.10-0.15	0.00-0.07	0.10-0.25
Axis diam. 0.8-1.0 mm	0.15-0.25	0.07-0.12	0.26-0.32
Axis diam. 1.0-2.0 mm	ca. 0.3	0.12-0.18	0.25-0.40
Axis diam. >2.0 mm	ca. 0.5	0.12-0.25	-
Polyps:			
Maximum height[f] (mm)	2.5	2.2	ca. 2.3
Number per cm	3-6	3-6	3+
Pairs of pinnules	6-7[g]	8-10	-

[a] Specimen may be part of a larger colony.
[b] Unbranched branchlets, rarely longer.
[c] On the same side of the axis.
[d] Most common condition italicized.
[e] Height of spines very variable, commonest size ranges shown.
[f] Including tentacles.
[g] As reported by Thomson (1910)

to stand out at right angles to the axis, but rather are inclined distally.

Remarks: Thomson (1910) reported that the polyps were often in subopposite pairs, with the pairs spaced at intervals of two lengths or more apart. He also noted that there were six or seven, pairs of pinnules on the tentacles.

Distribution: Known from off Ascension Island, 777 m. ("Challenger" Expedition), and from Cape Verde Islands, 394 m.

Dendrobrachia paucispina sp. nov.
FIGS 3-8, 12-13; Table 1

Material Examined: Off the southern coast of Western Australia: 125 nautical miles East of Cape Arid, 34°03′S, 125°31′E, 1011-1020 m, F/V "Adelaide Pearl", 31 July 1988, Coll. K. Gowlett-Holmes, K. Olsson, M. Cameron, syntypes: South Australian Museum SAM H715, 1 spec.; USNM 87769, 1 spec.; about 80 nautical miles SW of Pearson Island, 35°04′S, 133°35′E, 900-960 m, F/V "Comet", 13 April 1989, coll. K. Gowlett-Holmes, syntype: SAM H716, 1 spec.; about 100 nautical miles due west of Whidbey Point, 34°49′S, 133°07′E, 884-859 m, F/V "Longva III", coll. K. Gowlett-Holmes, 11 November 1989, syntypes: SAM H728, 1 spec.; USNM 87768, 1 spec.

Description: Colony planar, loosely branched, with some overlapping of adjacent branches; branchlets bilateral and very irregularly alternate; highest order branches usually not more than 3 cm long, 0.4-0.8 mm in diameter, on average about 1 cm apart on same side of lower order branches. Six, occasionally seven, rarely eight longitudinal axial ridges on branchlets, increasing in number on thicker branches. Spines sparse, often absent, arranged in one row per axial ridge where present. Spines not uniform in size and shape, but increasing in length on larger branches; about 0.1 mm long on branches 1 mm in diameter. Polyps bilateral, in alternate or subopposite pairs, 3-6 per cm.

Discussion: The type series consists of six specimens, all of which are to some degree bent over

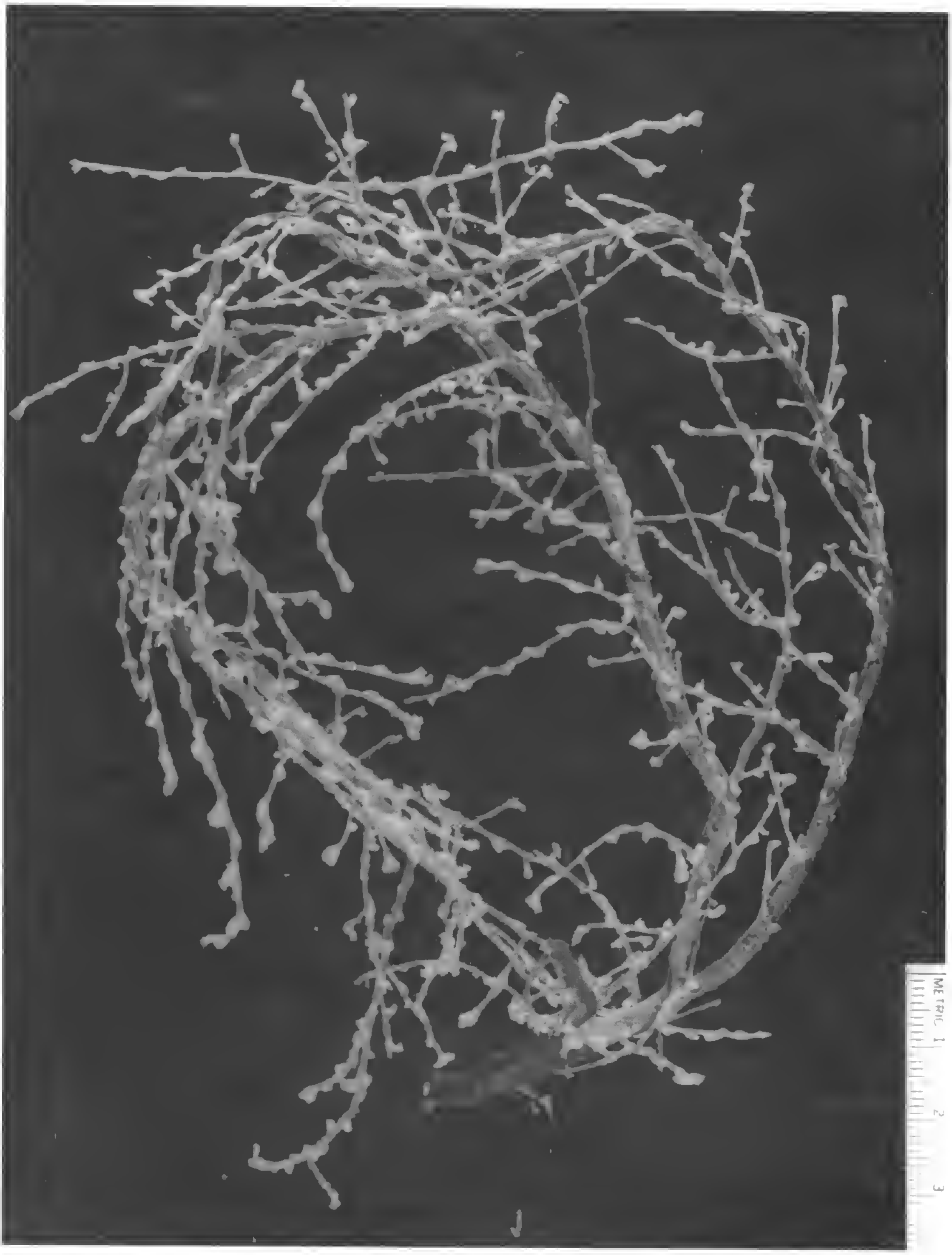


Fig. 3. *Dendrobrachia paucispina* sp. nov. Syntype colony SAM H715.

and twisted in the upper part of the corallum, a condition which may have resulted in part from preservation and storage in small containers. When unfolded into what was probably its natural shape, the largest colony is about 45 cm tall and 15 cm wide, with a basal stem diameter of 7.5 mm. The smallest colony is 15 cm tall and about 7 cm wide, with a basal stem diameter of about 2 mm.

A colony of medium size (SAM H715) is described in detail. This specimen is about 28 cm tall and 6 cm wide, and has a basal stem diameter of 4 × 4.3 mm (Fig. 3). The branching pattern of the corallum is generally planar with some overlapping of adjacent branches. The branching is irregular to about the 9th order. The highest order branching consists of small, relatively thin branchlets arranged in a very loose bilateral and alternating pattern. The smallest unbranched branchlets range in length from 0.4–3.0 cm ($\bar{x}$ = 1.47 cm, n = 23), and they are 0.4–0.6 mm in diameter. The average distance between the bases of adjacent branchlets and/or branches on the same side of a lower order branch is 9.0 mm (range 4–19 mm, n = 30). The average distance between adjacent branchlets and/or branches on opposite sides is 4.8 mm (range 3–8 mm, n = 9). The branch angles (delineated by the distal side of a branch and the lower order branch from which it arises) are generally greater than 45°.

At the tips of the smallest branchlets, the axial skeleton consists of six, occasionally seven, and rarely eight narrow longitudinal ridges separated by deep, u-shaped grooves (Fig. 4, top). The ridges increase in number on the thicker, older parts of the corallum (Fig. 4, bottom), are present on the stem and also faintly visible on the upper part of the holdfast. On branches 2–3 mm in diameter, 12 or more ridges can be seen in one lateral view.

Over most of the corallum, and particularly on branches less than 1 mm in diameter, the skeletal ridges are smooth (Fig. 5, top); however, in some places scattered spines occur in a single row along several of the ridges. On the smaller branchlets they take the form of small rounded elevations (Fig. 5, bottom); on the older branches they are more spine-like (Fig. 6). Where present, the spines occur on only one or a few of the ridges and never on all the ridges around the circumference of the axis. Although quite variable, the height of the spines is generally about 0.07 mm on a branchlet 0.6–0.8 mm in diameter, 0.07–0.12 mm on branches about 0.8–1.0 mm in diameter, and 0.12 to 0.18 mm on branches 1.0–2.0 mm in diameter. There are usually 3–5 spines per millimeter in each row. Spines are also found at the base of several of the small branchlets which arise directly from the stem or thicker branches. In these cases the spines can be 0.25 mm or more in height.

Polyps are present throughout the corallum. They are not arranged in a strictly regular order but are more abundant on the lateral and front sides of the branches (relative to the plane of the corallum). On many of the larger branches a narrow band of coenenchyme without polyps extends down the middle of the posterior side. On the branches the polyps are spaced irregularly (Fig. 7), sometimes unilaterally, and sometimes bilaterally with alternating or opposite pairs. Most polyps are about 5 mm apart, and there can be 3–6 polyps per centimeter depending on whether they are placed singly or in pairs. They are usually inclined distally, often with their adaxial side lying against the axis. The largest polyps are about 2.2 mm tall (including tentacles); the body column is about 1 mm in length (Fig. 8). On several polyps in which the tentacles were adequately expanded, 8–10 pairs of pinnules could be seen on each tentacle.

The remaining specimens in the type series are similar in most morphological features to the one described above. All the colonies have a typical planar branching pattern, with the highest order unbranched branchlets being not more than 3 cm long and spaced about 1 cm apart in a very loose bilateral and alternating fashion. In the larger colonies, there are infrequent fusions of some of the lower-order branches and the larger branches and stem have a distinctive golden, somewhat iridescent sheen.

From specimen to specimen, and even within a single colony — from branch to branch — differences can be seen in the occurrence, size, and density of the axial spines. In the two largest specimens (SAM H728 and USNM 87768), the spines are overall slightly smaller and sparser than those in the described colony. Furthermore, spines are only rarely present on branches of about 2 mm in diameter or more; however, the axial ridges remain distinct and can be seen on both the branches and the stem.

In another specimen (SAM H728, height 30 cm, basal stem diameter about 4 mm) spines are present on all parts of the corallum including the stem and basal plate; however, they are not uniformly distributed, are absent in some places, but present on all the axial ridges in other places. This variability in the occurrence of the axial spines is a characteristic feature of this species.

Remarks: Although the general form of the corallum of *D. paucispina* sp. nov. is very similar to that of *D. fallax*, this species can be differentiated on the basis of the very sparse number and relatively smaller size of the axial spines (Table 1). The

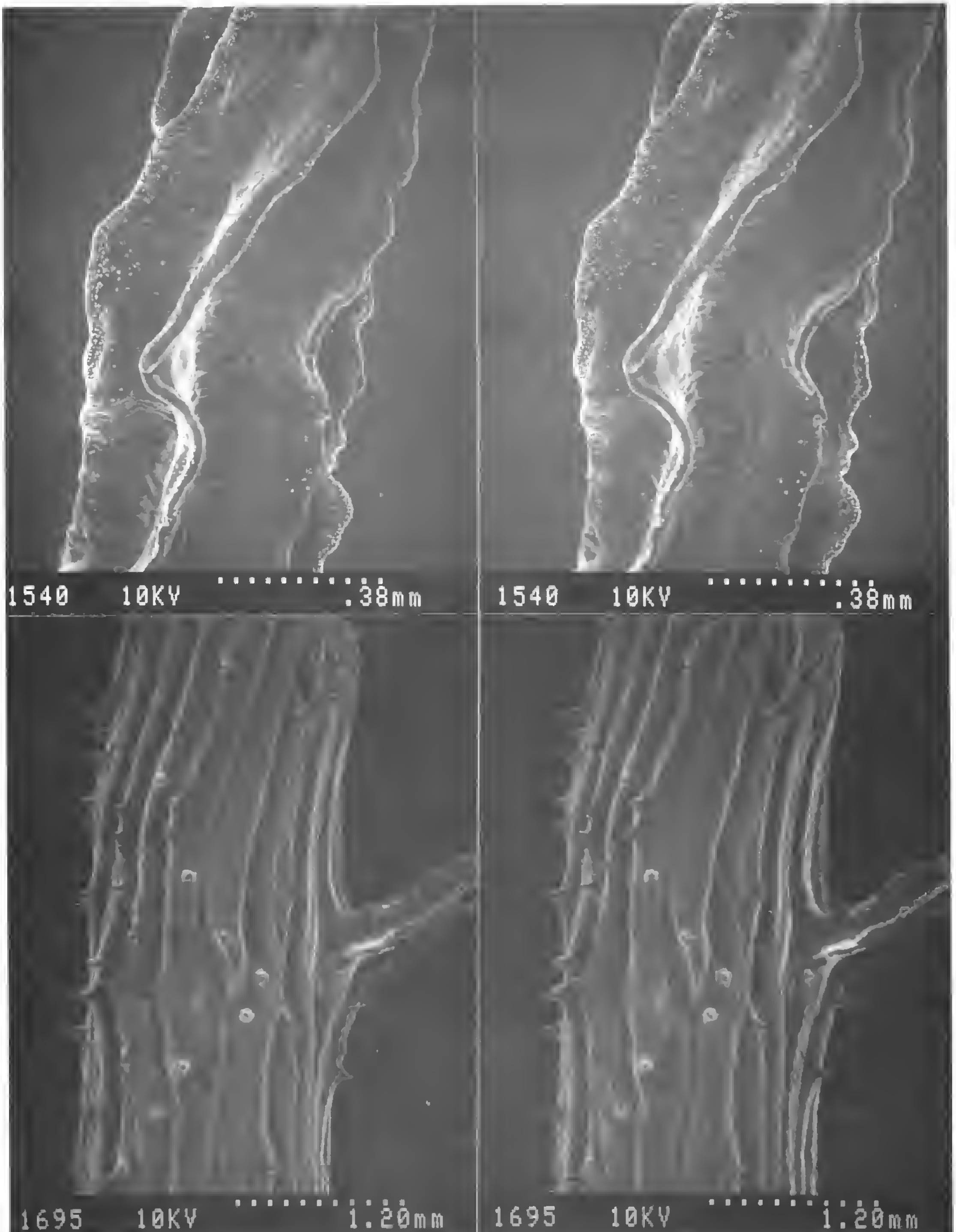


Fig. 4. *Dendrobrachia paucispina* sp. nov., axis. Top, lateral view of terminal twig; bottom, lateral view of larger branch SAM H715. Stereoscopic pairs, SEM.

Fig. 5. *Dendrobrachia paucispina* sp. nov., axis. Lateral views of terminal twigs, SAM H715. Stereoscopic pairs, SEM.

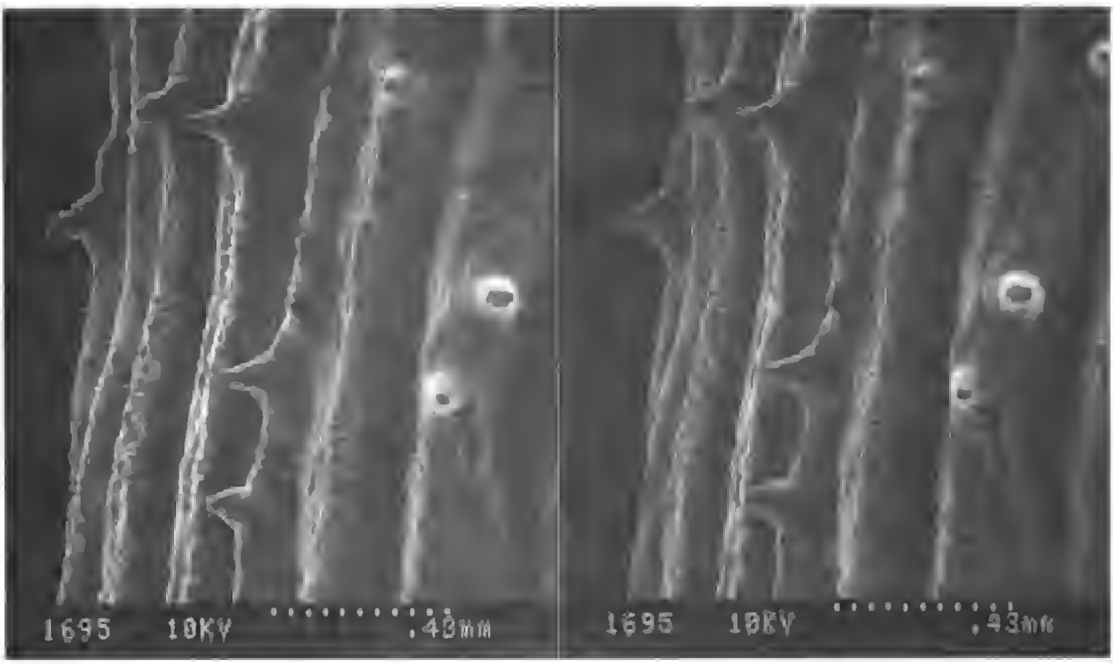


Fig. 6. *Dendrobrachia paucispina* sp. nov., axis. Lateral view of larger branch, SAM H715. Stereoscopic pair, SEM.

complete absence of spines on many parts of the axis is quite distinctive. Where present, and for branches of similar thickness, the spines in this species are only about one-half as large as those in *D. fallax*. Although in both species the smallest branchlets most commonly have six primary axial ridges, in *D. paucispina* sp.nov. there are occasionally seven and sometimes even eight ridges present. In contrast, in *D. fallax* there are occasionally five or seven ridges on the smallest branchlets. The polyps in *D. paucispina* sp. nov. and *D. fallax* appear to be similar in size and number; however, there is some evidence suggesting that the number of pairs of pinnules on the tentacles may be different in the two species. In this species there are eight-ten pairs of pinnules per tentacle. According to Thomson (1910), there are only six-seven pairs per tentacle in *D. fallax*.

Distribution: Known only from the Great Australian Bight, 884-1020 m, on the continental slope.

Dendrobrachia multispina sp. nov.
FIGS 9-11, Table 1

Material Examined: Straits of Florida, west of Cay Sal Bank, Bahamas, 23°51.9′ N, 80°42.7′ W, 1080-1089 m, R/V "Gerda" Sta. 1111, 30 April 1969. Holotype, USNM 87770.

Description: Colony planar, very sparsely branched; branchlets bilateral, very irregularly alternate; highest order branchlets usually not more than 3 cm long, 0.4-0.5 mm in diameter, on average 1.3 cm apart on same side of branches. Five longitudinal axial ridges on branchlets. Spines in rows on axial ridges, one row per ridge on smallest branchlets, multiple rows on larger branchlets and branches. Spines not uniform in size or shape, becoming tall and acicular on larger branchlets and branches; about 0.3 mm long on branches about 1 mm in diameter. Polyps mostly bilateral and alternate, 3 per cm.

Discussion: The type specimen lacks a basal holdfast and may have been broken off a larger colony. The upper portion of the specimen is bent, perhaps due to preservation (Fig. 9). With the branches straightened and extended vertically, the corallum is about 19 cm high and 7 cm wide. The diameter at the basal end of the "stem" is 1.4 mm. The colony is very sparsely and openly branched in an irregular bilateral fashion. The average distance between the bases of adjacent branchlets and/or branches on the same side of the lower order branches is 13 mm (range 8-21 mm, n = 24). The

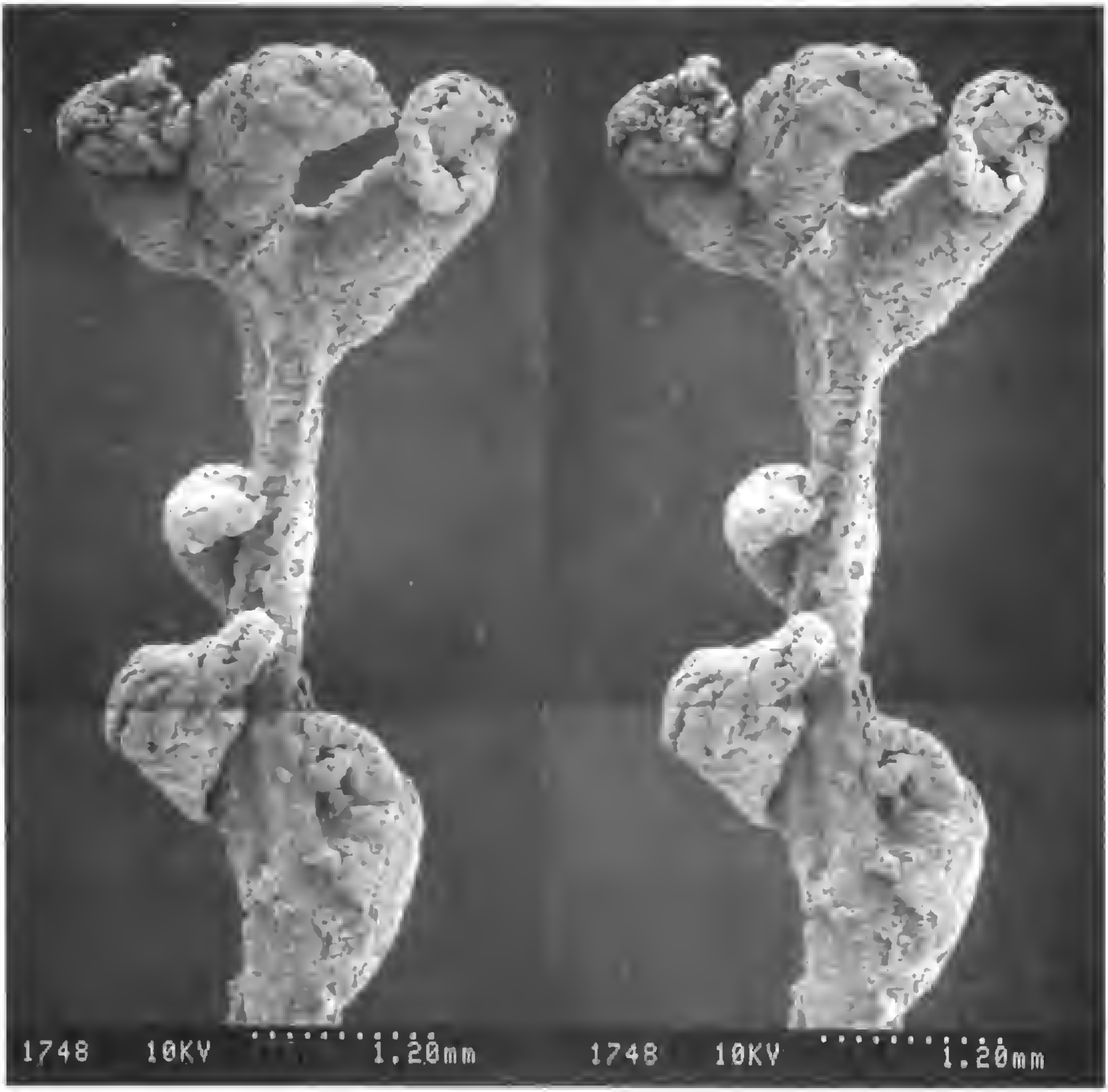


Fig. 7. *Dendrobrachia paucispina* sp. nov. Tip of terminal branch with polyps intact, critical-point dried, SAM H715. Composite stereoscopic pair, SEM.

average distance between adjacent branchlets and/or branches on opposite sides is 6 mm (range 1-16 mm, n = 22). The branch angles are mostly 60° or more. The smallest unbranched branchlets range in length from 0.7-3.1 cm ($\bar{x}$ = 1.5 cm, n = 12) and they are relatively stiff and straight. They are about 0.4-0.5 mm in diameter.

At the tips of the smallest branchlets, the axial skeleton consists of five narrow longitudinal ridges separated by wide v-shaped grooves. For a distance of 0.5-2 cm from the tips of the branchlets the ridges are smooth or have only small irregularly rounded or triangular elevations which are generally not more than 0.07 mm high (Fig. 10). With increasing thickness of the branchlets these develop into spines which eventually become relatively tall and acicular, the ridges become wider and lobe-like, and the grooves become relatively narrow (Fig. 11, top). Multiple rows of spines develop on the surface of the enlarged ridges. In some places two relatively straight rows of spines are positioned along the edges of the ridges adjacent to the grooves with additional irregular rows or scattered spines occurring between the edge rows. Overall, the axis

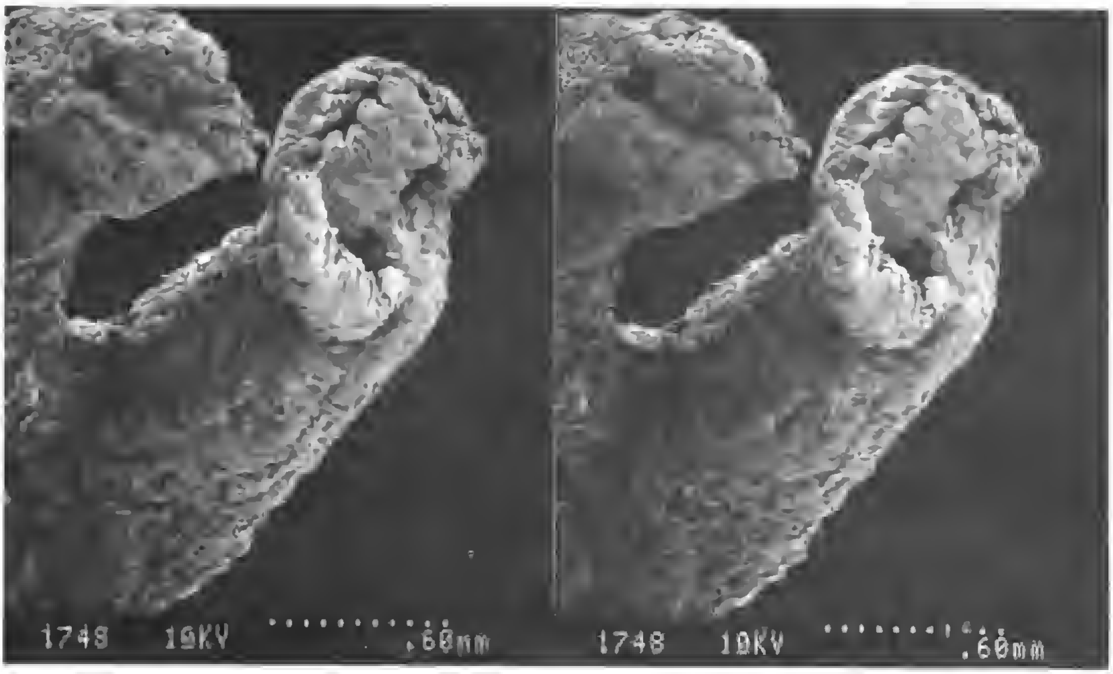


Fig. 8. *Dendrobrachia paucispina* sp. nov. Single polyp, critical-point dried, SAM H715. Stereoscopic pair, SEM.

becomes quite spinose; however, remnants of the five primary grooves, although quite narrow, remain recognisable, even at the base of the corallum.

The spines are not uniform in size or shape from branchlet to branchlet. They stand out at right angles to the axis and often are slightly crooked. The height of the spines is 0.10–0.25 mm on branchlets 0.6–0.8 mm in diameter (Fig. 11, bottom), 0.26–0.32 on branches about 0.8–1.0 mm in diameter, and up to 0.4 mm on branches 1.0–1.2 mm in diameter. The largest spines are relatively narrow, about 0.05 mm in diameter at their center. There are usually four or five, sometimes six spines per millimeter in each row. Occasionally the spines are slightly more developed at the base of small branchlets arising directly from the stem and thicker branches.

Polyps of this specimen are poorly preserved. They are arranged irregularly, in a somewhat bilateral pattern. There appear to be about 3 per centimeter. The largest polyps are about 2.3 mm tall (including tentacles); the tentacles are about 0.8–1.0 mm long.

Remarks: In size and general appearance *D. multispina* sp. nov. is similar to *D. fallax* and *D. paucispina* sp. nov. All have a somewhat planar corallum with rather irregular, but generally bilateral and alternating branching. The branching of the corallum of *D. multispina* sp. nov. is slightly more sparse and open, but this may not be typical, considering that the specimen may only be part of a larger colony. The taxonomic character in which this species differs consistently from the other two species is the greater development of the axial spines. In this species the spines on the larger branchlets and branches develop in multiple rows along the axial ridges, whereas in the other two species there is only one row of spines per ridge. The spines in *D. multispina* sp. nov. are also relatively larger and more crowded together than in the other two species (Table 1). In addition, in *D. multispina* sp. nov. the number of primary skeletal ridges on the branchlets is consistently five throughout the corallum, whereas in *D. fallax* it is usually six, occasionally five or seven, and in *D. paucispina* sp. nov. it is usually six, occasionally seven, and rarely eight.

Distribution: Known only from the type locality.

Anatomy and Histology

Anatomy and histology have not been described for very many species of Octocorallia, and much of the published information deals with a few pennatulacean species. Hickson (1895b) described the anatomy of *Alcyonium digitatum* Linnaeus,

Fig. 9. *Dendrobrachia multispina* sp. nov. Holotype colony, USNM 87770.

Bouillon & Houvenaghel-Crevecoeur (1970) described the anatomy and histology of *Heliopora coerulea* (Pallas), and Bayer & Muzik (1976a) described the general structure of the solitary *Taiaroa tauhou* Bayer & Muzik.

Among the gorgonaceans, the structure of *Pseudoplexaura crassa* Wright & Studer was investigated in considerable detail by Chester (1913), and that of *Plexaura homomalla* (Esper) by Bayer (1974). The anatomy and histology of those species conform in general with those of all other gorgonaceans the structure of which has been described.

The anatomy of the polyps of all monomorphic octocoral species and of the autozooids of dimorphic species is remarkably uniform. As this basic form has been described and illustrated adequately in general treatises (e.g., Hyman 1940; Bayer 1956) as well as in specialized accounts (Hickson 1895b; Chester 1913; Bayer 1974; Bayer *et al.* 1983), it need not be repeated here. The polyps of *Dendrobrachia* conform to the general gorgonacean pattern. Paraffin serial cross-sections of a polyp of *Dendrobrachia paucispina* sp. nov. clearly show that the general form corresponds to the usual gorgonacean pattern, differing in only

Fig. 10. *Dendrobrachia multispina* sp. nov., axis. Lateral views of terminal twig USNM 87770. Stereoscopic pairs, SEM.

minor details. As the specimens were not prepared with anatomical and histological investigation in mind, fixation is adequate only for demonstration of gross anatomy and a very superficial investigation of histology.

From Fig. 12 it is clearly seen that the polyps of *Dendrobrachia* have the usual four couples of complete mesenteries and a single siphonoglyph. The arrangement of longitudinal retractor muscles is, as usual, on the sulcal face of the mesenteries, but the retractors of the asulcal and sulcal mesenteries are relatively weak (at least at the level of the body that was sectioned) and development of mesogloeal plates on the asulacal side of the four lateral mesenteries (Figs 12, 13) is a clear indication that muscle fibers are present on both faces of at least the lateral mesenteries.

The siphonoglyph is well developed and the epithelium of the pharynx at its upper end is thrown into about 10 longitudinal folds, similar to the condition in *Alcyonium* observed by Hickson (1895b). These seem to fade out proximad, where they give way to transverse folding of the pharyngeal wall probably related to shortening of the pharynx resulting from contraction.

The epidermis (Fig. 13) is composed of the usual tall, obconic cover cells (cf. Chester 1913; Bayer 1974), thrown into conspicuous lobes and covered by delicate cuticle, which in many places has been torn off during processing. Nematocysts of unknown type but probably atrichous isorhizas are very widely scattered in the epidermis of the body wall, not densely clustered in batteries as is the case in Antipatharia (van Pesch 1914).

The mesogloea of the body wall of the polyps is unusual in that it appears to consist of two layers, the inner stained pink as usual in haematoxylin-eosin, the outer, somewhat thinner, dark purple. However, as disruption of tissues during the sectioning process separates the two layers here and there, it is more likely that the darkly stained outer layer is, in fact, a basement membrane of the epidermis.

The gastrodermis of the body wall is unusually thick, in some places nearly or quite as thick as the epidermis, and composed of elongate, spindle-shaped cells. In the immediate vicinity of the mesenteries, narrow ridges of mesogloea extend into the gastrodermis, strongly suggesting the presence of longitudinal muscles.

Affinities within the Octocorallia

It is not insignificant that the curator of invertebrates of the South Australian Museum associated *Dendrobrachia* with *Chrysogorgia*. Often, superficial similarity may reflect more fundamental relationships.

The absence of calcareous sclerites in *Dendrobrachia* eliminates one of the classic characters in gorgonacean classification, leaving only the nature of the axial supporting skeleton as a clue to relationships. Among the gorgonians, only two species of *Trichogorgia* lack sclerites, one of them having been the basis for the genus *Malacogorgia* and family Malacogorgiidae (Hickson 1904). Apart from the complete absence of calcareous skeleton, *Malacogorgia capensis* is identical to *Trichogorgia flexilis* and both have long been placed in the family Chrysogorgiidae on the basis of the typical chrysogorgiid sclerites of *T. flexilis* (Kükenthal 1924; Bayer & Muzik 1976b). *Trichogorgia viola* Deichmann, 1936, from the Gulf of Mexico is morphologically similar and also has sclerites of the chrysogorgiid type. Colonies of *Trichogorgia lyra* Bayer & Muzik, 1976, from the southwestern Caribbean, which are not unlike *Malacogorgia* (=*Trichogorgia*) *capensis* in some respects, like it lack sclerites but have calcareous deposits in the axis.

Gorgonacean families with an unjointed, more or less calcified axial skeleton without a hollow core are Primnoidae, Ellisellidae, Ifalukellidae, and Chrysogorgiidae. Among these, only *Trichogorgia capensis* in the Chrysogorgiidae has an axis devoid of calcareous deposits.

The axis of *Dendrobrachia* lacks calcification as well as a hollow core, thus resembling that of *Malacogorgia* (=*Trichogorgia*) *capensis* and, like it, also lacks sclerites. Some species of *Plumigorgia* are very scantily provided with sclerites of very small size and considerably different from the prevalent chrysogorgiid type, and *Ifalukella yanii* Bayer has so few as to be virtually sclerite-free. However, both genera are inhabitants of shallow, reef-associated waters, and the axis in both develops a strong, even massive, calcareous holdfast. In the case of *Ifalukella*, the holdfast has conspicuous longitudinal grooves and ridges that are sharply serrate or laciniate, but the arborescent part of the axis is only weakly ridged, as in many other gorgonacean genera (Bayer 1955). The holdfast of *Dendrobrachia* is not calcified and forms a minimally spreading encrustation on solid objects.

Anatomically, the polyps of *Dendrobrachia* agree with those of *Chrysogorgia*, *Stephanogorgia*, *Trichogorgia* and *Ifalukella*. Unfortunately, the anatomy and histology of those genera have not been described, but direct comparison with serial sections of *Chrysogorgia elegans* (Verrill), *Stephanogorgia faulkneri* (Bayer), *Trichogorgia lyra* Bayer & Muzik, and *Ifalukella yanii* Bayer reveals similar features.

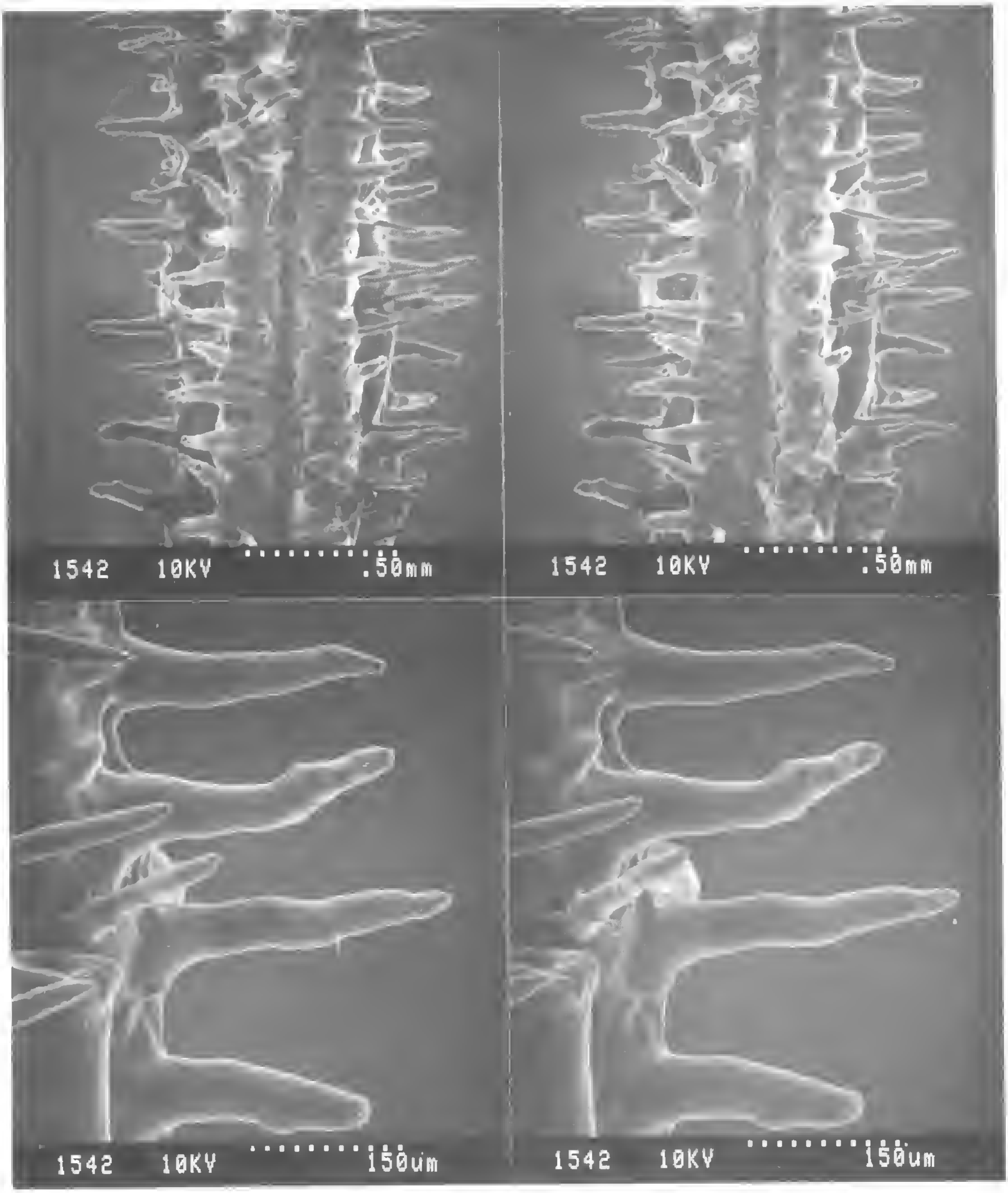


Fig. 11. *Dendrobrachia multispina* sp. nov., axis. Top, lateral view of larger branchlet; bottom, axial spines of same USNM 87770. Stereoscopic pairs, SEM.

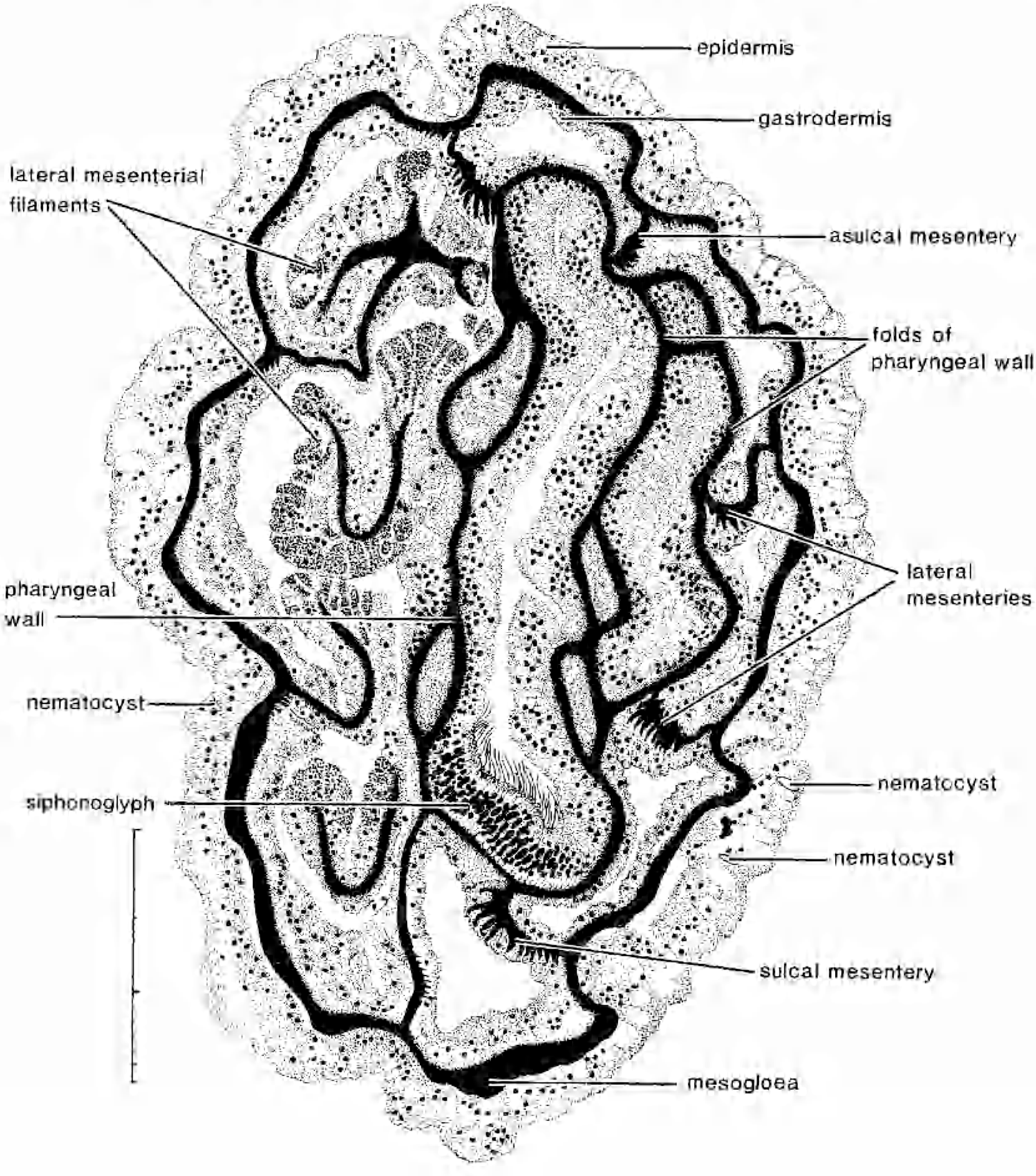
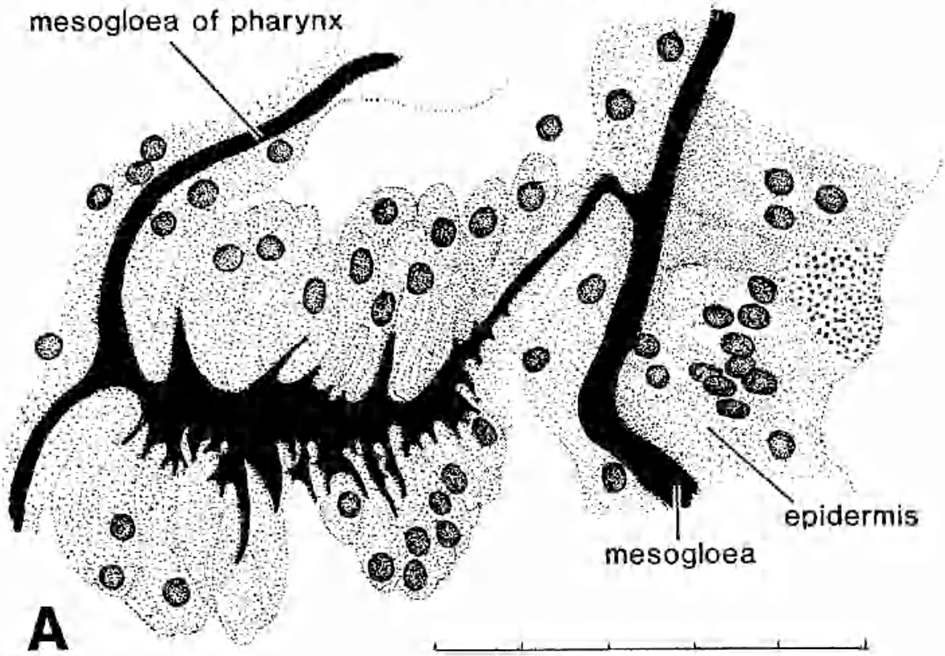
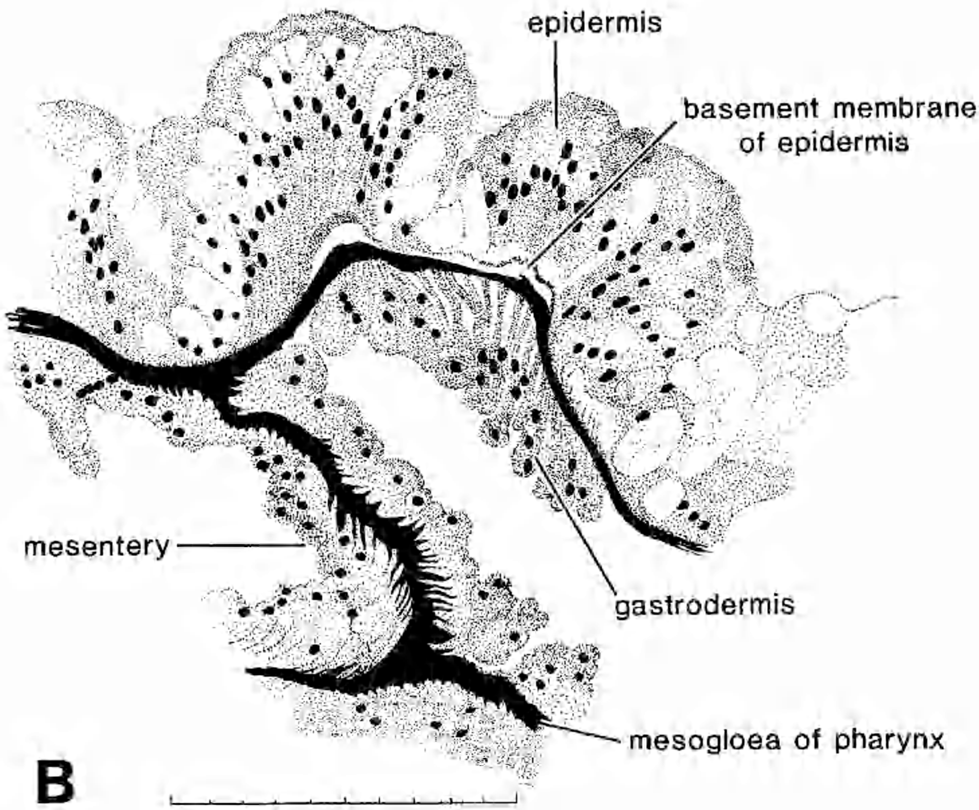


Fig. 12. *Dendrobrachia paucispina* sp. nov. Cross section of polyp, somewhat oblique, at level of pharynx. Scale = 0.15 mm.


mesogloea of pharynx
epidermis
mesogloea

A


epidermis
basement membrane
of epidermis
mesentery
gastrodermis
mesogloea of pharynx

B

In spite of the general similarity of the polyps of *Dendrobrachia* with those of the uncalcified species of Chryosogorgiidae, the unique nature of the axial skeleton convinces us that the family Dendrobrachiidae should be maintained, at least until material becomes available for a more comprehensive investigation and comparison of anatomical and histological features of all the species involved.

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Fig. 13. *Dendrobrachia paucispina* sp. nov., A. Cross section of body wall with mesentery showing longitudinal mesogloeal plates for insertion of retractor muscles on both faces; B. Cross section of body wall showing epidermal lobes and mesentery with longitudinal mesogloeal plates for retractor muscles on both faces. Scale at A = 0.05 mm; scale at B = 0.1 mm.

THE DISPERSED CUTICULAR FLORAS OF SOUTH AUSTRALIAN TERTIARY COALFIELDS, PART 1: SEDAN

*BY A. I. ROWETT**

Summary

Dispersed cuticles were recovered from the three seams of the Sedan Coalfield and sixty-two parataxa have been identified. The floras of the two younger lignite seams are distinct from the underlying lignitic clay. The lignites are dominated by Proteaceae cuticle types with one cuticle type, identified as the cuticle of *Banksieaephyllum laeve,* i.e. *Banksieaephyllum* aff. B. *laeve* in abundance. The older lignite seam is distinguished by a large monospecific Myrtaceae component and a cuticle type identified as aff. *Agathis* (Araucariaceae). Other families represented in both seams include the Casuarinaceae, Elaeocarpaceae, Myrtaceae and Podocarpaceae. The flora of the under-lying lignitic clay is dominated by Lauraceae cuticle types.

The presence of *Banksieaephyllum* aff. B. *laeve* in the Sedan lignites suggests either an Oligocene-Miocene age for the lithotype or a longer stratigraphic range (extended lower limit) for the leaf-fossil.

KEY WORDS: Palaeobotany, Tertiary, Eocene, dispersed cuticles, Sedan, South Australia